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## The mechanism of seed-dispersal in *Polygonum virginianum* \*

HOWARD SPRAGUE REED AND ISADORE SMOOT

The achenes of *Polygonum virginianum* Linnaeus have a particularly efficient mode of dispersal. The long two-parted styles are persistent and become lignified during the process of development. If, after maturity, these projecting styles are struck by any object with sufficient impact, the achenes are thrown off with force enough to carry them a distance of three or four meters.

During windy weather the tall, slender racemes are blown against each other and against the strong stems of plants like *Phytolacca* and *Sambucus*, with which this species of *Polygonum* is associated. The impact thus produced is sufficient to throw off the mature achenes without the agency of animals. Nevertheless, animals are very efficient means of dissemination, for, if they do touch the trigger-like styles, the achenes are thrown with some force against the body of the animal, where they cling, the sharp, reflexed points of the style (see fig. 1) becoming fixed in the hair, or fleece, and they may thus be carried some distance.

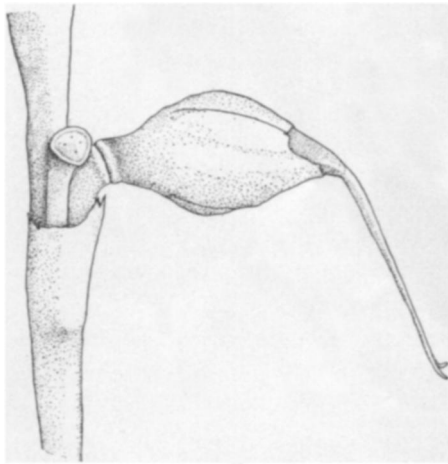


FIG. 1. A mature achene of *Polygonum virginianum*.

All botanical text-books give examples of fruits and seeds which are forcibly ejected when ripe. In most cases the force is due to some property of the ripened wall of the gynoecium. The ejection of the achenes of *Polygonum virginianum* is unique in that the requisite force is derived from a tension in the pedicel.

\* Contribution No. 9 from the Botanical Laboratory of the University of Missouri.

Hildebrand ('73) mentions this plant as one whose achenes are transported by animals, but appears not to have noticed their forcible expulsion. He mentions only the hooked styles which fasten the achenes to the hair, or fleece, of animals.

Kerner ('95) described it as a "catapult fruit." He perceived the separation-layer in the pedicel, but gave no satisfactory explanation of the manner in which ejection was accomplished. His account (2: 842) might lead one to think that the tension was produced by the cells of the cortical parenchyma. We have not found it to be so.

The devices of the plant for dispersing its fruits have been noted by Beal ('98), but no explanation was given.

This paper relates the results of a histological study of the tissues in question. Since the achenes fly off with a force entirely disproportionate to that which strikes them, it may be assumed that there is some tension existing in the pedicels which, when released, throws the achenes from the plant. It has been supposed that the existing tension was given by changes in the tissues of the pedicel as they became dry. The attempt was made to discover whether changes might be found in the structure or arrangement of these tissues sufficient to account for the phenomenon of dispersal.

The material studied was collected near Columbia, Missouri, in the autumn of 1904, and during the summer and autumn of 1905. All stages were obtained, from the first formation of the raceme to the mature achene. The killing fluids used were mercuric-bichloride in 95 per cent. alcohol, Mann's picro-corrosive fluid, chrom-acetic acid, and Worcester's killing fluid. The older material was embedded in celloidin and the younger in paraffin. The stains used were fuchsin-iodine-green, iron-alum-haematoxylin and safranin, and Delafield's haematoxylin.

*P. virginianum* constitutes the only member of the subgenus *Tovara*, according to Small ('95). The plants are herbaceous annuals, somewhat woody at the base. When the species of this genus are arranged according to their histological structure, *P. virginianum* appears to stand about midway in the series. The epidermis, like that of nearly all the other species, consists of a single row of cells. The hypodermal tissues are not so well developed

as in those species, like *P. alpinum*, which grow in dry situations, but is better developed than in species like *P. scandens*, which grow in wet localities. In comparison with the other species, the stereome cylinder of *P. virginianum* is compact and well developed. The elements are small and very thick-walled, therefore they may be regarded as contributing much of the rigidity necessary to support these tall, slender stems.

The phloem bundles, although small, do not disintegrate as they do in some other species. The xylem forms a comparatively wide zone and contributes a great deal of mechanical strength to the stem. It consists of five different elements, namely, woody fibers, tracheids, spiral vessels, annular vessels, and wood parenchyma which gradually merges into the pith.

The pith consists of large cells, hexagonal in longitudinal section. Unlike the same kind of cells in other species, they are usually broader than they are high.

In a general way, the form and structure of the tissues in the pedicel are similar to those in the stem. The most constant difference between them is that some of the individual elements of the pedicels are more elongated than the corresponding elements in the stems. About 0.75 mm. below the base of the achene, the tissues of the mature pedicel are interrupted by a crescent-shaped "separation-layer." It is by virtue of this layer that the fracture is readily effected when the achenes are thrown off. Its characters will be more fully discussed later. The cells of the epidermis, which at first are parallelopipeds, like those of the cauline epidermis, become stretched from four to six times their original length as the pedicel develops.

The zones of stereome and woody tissue are reduced in width and number of elements. The zone of stereome tissue is usually thicker on the concave side of the pedicel than on the convex side (fig. 3). In all probability this may be regarded as a regulatory thickening such as Newcombe ('95) described for mechanical tissues in general.

The fibro-vascular tissue never forms a zone of any considerable thickness. There is no evidence that the phloem bundles ever disintegrate, but are continuous throughout the pedicel, although they decrease in size beyond the separation-layer. Opposite each

phloem bundle there is a group of from five to seven annular and spiral vessels. Between these groups of vessels the space is filled up with wood parenchyma in such a way as to form a continuous cylinder. The woody tissue never reaches any considerable development, hence this cylinder is thin-walled even at maturity.

Just above the separation layer the fibro-vascular bundles branch dichotomously. The outer branches continue their course into the

persistent calyx, the inner branches meet and fuse directly below the achene.

(Figs. 2 and 3.)

A longitudinal section of the pedicel shows that the cells of the pith differ in size and shape from the corresponding cells in the stem. The latter were described as being hexagonal in longitudinal section and distinctly broader than they were high. The pith cells in the pedicels, on the other hand, are rectangular in longitudinal section and have a length from two to six times as great as their width (fig. 5). The longest cells are formed near the base of the pedicel; the shortest ones near the separation-layer. Subsequent

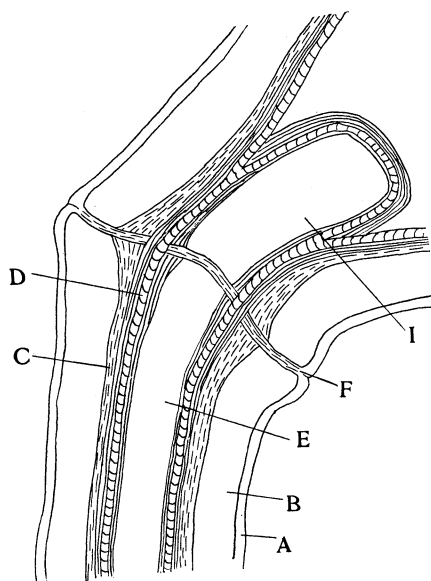


FIG. 2. Diagram of a median longitudinal section of a young pedicel shortly after the differentiation of the separation-layer. A, epidermis; B, cortex; C, sclerenchyma; D, fibro-vascular bundles; E, pith; F, separation-layer; I, cushion of thin-walled pith-cells.

changes in the form and structure of the pith cells will be described later.

The achene is attached to the distal end of the pedicel by a broad base, which does not become weakened as the fruit matures. This accounts for the fact that when the achene is cast off the fracture occurs, not at its base, but at the specially developed separation-layer mentioned above.

The wall of the achene consists of two layers. The outer and

thicker layer is composed of compact sclerenchyma elements, which have been described by Sirrine ('94), and the inner layer is composed of long, woody fibers, which are in close contact with the sclerenchyma wall. At the apex of the achene the fibers of the inner wall are continued outward and downward, forming the tissue of the persistent style. The whole structure of the achene gives to it sufficient mechanical strength to resist fracture at all points except the specially constructed separation-layer.

Certain indications of a separation-layer in the pedicel are evident from a very early stage. The youngest flower-stalks ex-

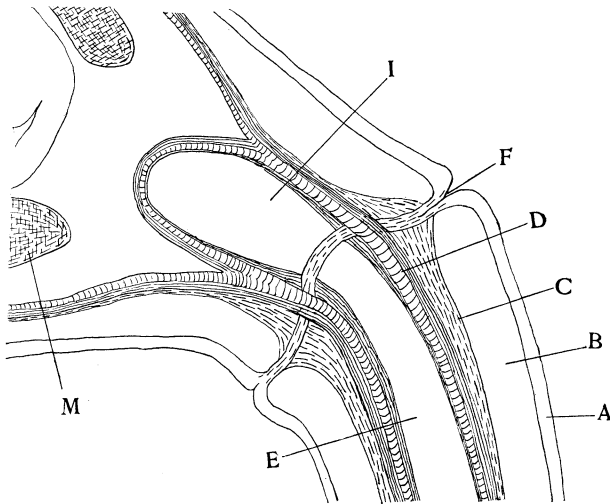


FIG. 3. Diagram of a median longitudinal section of a pedicel at the time of maturity. *A*, epidermis; *B*, cortex; *C*, sclerenchyma; *D*, fibro-vascular bundles; *E*, pith; *F*, separation-layer; *I*, cushion of thin-walled pith-cells; *M*, sclerenchyma-layer of achene-wall.

amined seemed to indicate that the pollen-mother-cells had recently accomplished the second division. In such sections one may discern a zone of short cells extending across the pedicel a short distance beneath the base of the macrosporangium. The cells of this zone are thin-walled and parenchymatous like the other cells of the young pedicel. At the same time, or very shortly afterward, the pedicel is slightly constricted in the region of this zone.

As the flower approaches the time of blossoming the cells of the pedicel undergo differentiation into the tissues described above.

At the time when the gynoecium is pollinated, it has been raised by intercalary growth nearly 0.5 mm. above the place where the zone of short cells arose. Simultaneously, a well-defined separation-layer may be distinguished in the midst of this zone. It consists of two rows of very short cells (fig. 4), which come in contact with the epidermis of the pedicel at the constriction which appeared somewhat earlier. This layer has the general form of a very low, flat-topped dome (fig. 2). All the tissues of the pedicel, except the fibro-vascular bundles, are intersected by this double row of cells. As the superficial notch deepens, the mar-

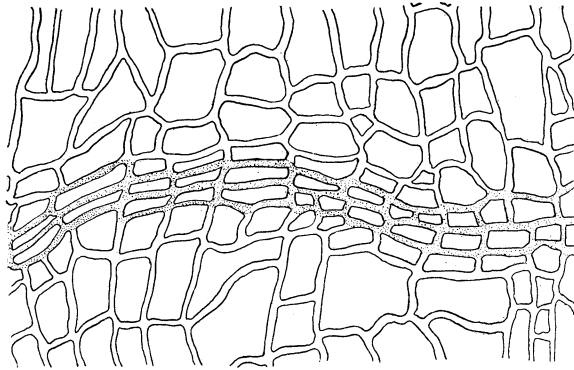


FIG. 4. Section showing the separation-layer shortly after it is differentiated.

gins of these layers are brought into contact with the epidermal layers, and their cells become cutinized.

Following the differentiation of the separation-layer, there is instituted a series of changes in the tissues of the pedicel. The pith-cells for some distance on the proximal side of the layer begin to elongate, and at the same time their walls become considerably thickened. The cell-elongation and wall-thickening appear to start about the same time; ultimately the greatest wall-thickness is reached in the immediate vicinity of the separation-layer. The result is that the separation-layer is pushed upward in the middle, giving it the form of a higher and more sharply pointed dome than formerly (fig. 3). Some notion of the amount of elongation may be formed by noting the increase of curvature in the separation-layer as the time of maturity approaches (figs. 2 and 3). Figure 6, T, represents the thickness of walls of pith-cells in the imme-

mediate vicinity of the separation-layer, as compared with the same kind of cells half way down the pedicel, shown in figure 5. On the distal side of the separation-layer, the walls of the pith-cells remain thin and unchanged (fig. 7), except for a few rows in the immediate vicinity of the layer. The slender, pointed cells of this tissue are interpreted to mean that they have grown under pressure, which caused them to glide between neighboring cells, as opportunity offered. The pressure involved was produced by the elongation of the thick-walled cells. By referring to figure 5 it will be seen that the rigid, thick-walled cells of the pith do not glide between each other. The mechanical tissues develop regularly and form the cylinder described above.

The fibro-vascular system may be compared to a thin-walled, inelastic cylinder (fig. 3, D), inside of which the elongating pith-cells (fig. 3, E) act like a piston moving against the soft, spongy, pith-cells (fig. 3, I) in the closed end of the rigid cylinder. The cushion of thin-walled cells is thus analogous to a compressed spring (one end of which presses against the achene and the other against the separation-layer). So long as the structure is undisturbed, the fibro-vascular cylinder restrains the elongating force of the pith column, but when the rigid style is struck by sufficient force, the strained walls of the cylinder break at the separation-layer and the compressed cushion of cells, suddenly expanding like a released spring, throws the achene off with considerable force. The invariable breaking of the fibrovascular bundles at the separation-layer is not hard to explain. An examination of a

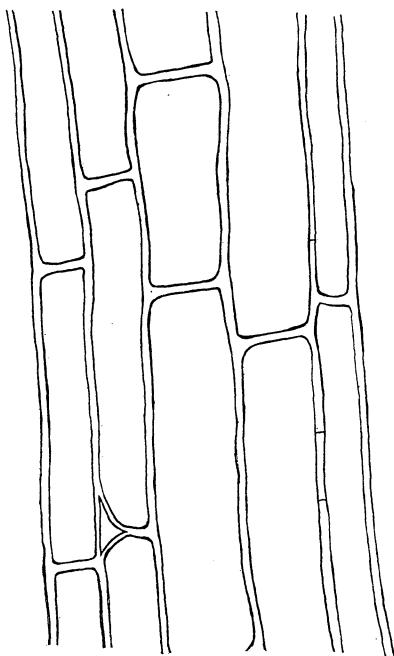


FIG. 5. Longitudinal section of pith taken about midway between the base and apex of the pedicel.



longitudinal section (fig. 3) shows that the reinforcing sclerenchyma-tissue is intersected by the separation-layer, thus materially weakening the mechanical tissue at that point.

Many longitudinal sections show a splitting of the marginal portion of the separation-layer as the fruits approach maturity. This was interpreted to mean that the cells of the cortex had lost part of their water content, and consequently had shrunk. When the cortical layer is thus cleft, the subsequent ejection of the

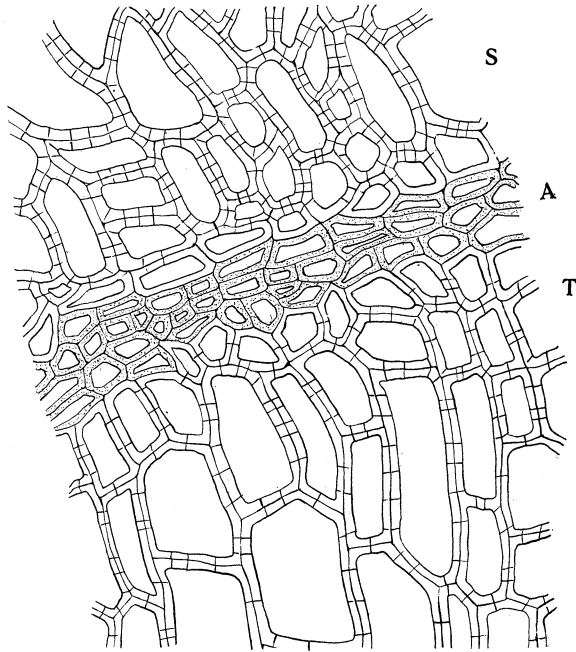


FIG. 6. Longitudinal section of pith at the separation-layer. *A*, separation-layer; *S*, pith-cells on distal side of separation-layer; *T*, pith-cells on proximal side of separation-layer.

achene is entirely dependent on the pith and mechanical tissue. The careful examination of several hundred sections failed to give any evidence which would confirm Kerner's statement that the cells of the cortical parenchyma become lignified. On the contrary, we found that the cortex plays no part whatever in producing the tension which ejects the fruit.

In order to learn whether any of the tissues of the pedicel were hygroscopic, they were subjected to moisture, with subse-

quent drying. Several mature racemes were placed in a moist chamber with a saturated atmosphere and allowed to remain there for four days, during which time the achenes remained attached. The racemes were then removed and placed in an oven, heated to

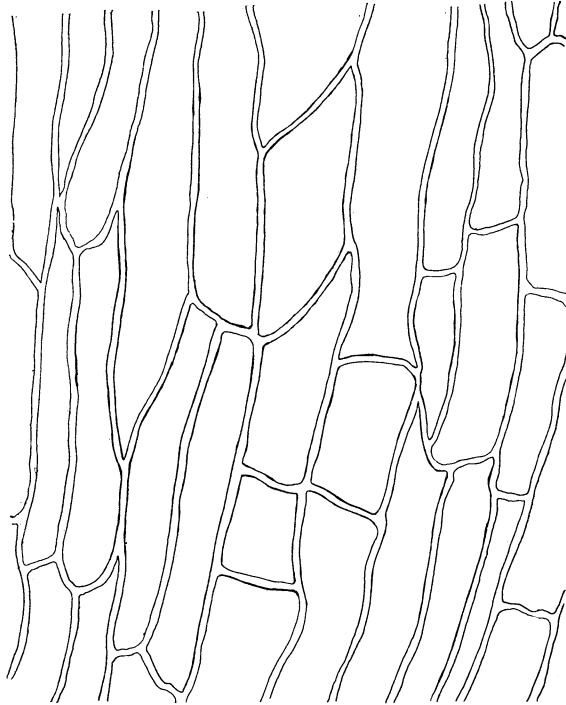


FIG. 7. Longitudinal section of thin-walled pith-cells which form the cushion (*cf.* figures 2 and 3, *I*).

75 degrees C. After seven hours they were again examined, but the effect of the drying had not been sufficient to detach any of the achenes.

The phenomenon of dispersal awaits an impact strong enough to break the fibrovascular cylinder and release the compressed cushion of cells. It is principally dependent on three things — a specially developed “separation-layer”; the existence of a longitudinal tension between the pith-column and the investing fibrovascular cylinder; and a blow on the achene analogous to the pull on the trigger which discharges a gun.

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